The retention of fish larvae in estuaries: among-tide variability at Beaufort Inlet, North Carolina, USA

Jean-Christophe Joyeux

North Carolina State University, Department of Zoology, Box 7617, Raleigh, NC 27695, USA.
Correspondence address: Universidade Federal do Espírito Santo, Departamento de Ecologia e Recursos Naturais,
29069–900 Vitória, ES, Brazil. E-mail: joyeux@npd.ufes.br

Sixty-eight tides were sampled consecutively to study the retention of fish larvae transported into estuaries. The experiment was conducted at Beaufort Inlet, North Carolina, USA, in March 1996. The inlet is primarily tide-driven and meteorological forcing has a minor influence. Four species of winter-spawning fish were abundant in the samples: Atlantic menhaden, *Brevoortia tyrannus*; Atlantic croaker, *Micropogonias undulatus*; spot, *Leiostomus xanthurus*; and pinfish, *Lagodon rhomboides*. Across-shore winds significantly affected flow and physico-chemical characteristics of the water. Across-shore winds also positively influenced the larval retention provided larvae did not present a clear tidal rhythm of vertical migration within the water column and that winds pushed in the water during flood tides. The retention of larvae migrating vertically in respect to the direction of the flow was independent of meteorological forcing of the water.

INTRODUCTION

The immigration of larval fish into estuaries from the ocean remains inadequately understood (Miller et al., 1984; Miller, 1988). In fact, the high biotic homogeneity of estuaries strongly contrasts with an important variability in hydrodynamics (Lyczkowski-Shultz et al., 1990), from river-dominated (river mouths of drowned river valleys) to tide-dominated (inlets into brackish lagoons), or even ocean-dominated (hypersaline lagoons). One of the mechanisms proposed for estuarine recruitment of plankton is that organisms exhibit vertical movements within the water column to take advantage of favourable tidal currents (selective tidal stream transport, TST; Creutzberg et al., 1978; Weihs, 1978). Vertical migration in phase with flow direction appears especially appropriate to penetrate and remain in stratified estuaries (for example, in systems where outflow is significant). Another proposed mechanism is that non-tidal flows induced by episodic meteorological events can provide favourable up-estuary currents (Shenker et al., 1993; Thorrold et al., 1994; Eggleston & Armstrong, 1995; Hettler et al., 1997). The coincidental occurrence of these events with the arrival of pulses of larvae at estuaries emerges as a potential source of interannual variability in entry and retention of larvae (Philippart et al., 1996; Hettler et al., 1997). This alternative to tidal transport may be especially appropriate for species that do not migrate vertically with the tide (Wooldridge & Loubser, 1996).

In shallow estuarine systems such as the Pamlico Sound, surface waters move in the same direction as the wind (Pietrafesa & Janowitz, 1988; Pietrafesa et al., 1986). Changes in wind velocity and direction induce adjustments of the water level within and outside the Sound. Strong winds may cause extended flood or ebb tidal events when the water rises on one side of the barrier and falls on the other side (Chao & Pietrafesa, 1980; Pietrafesa

& Janowitz, 1988). In multiple-inlet systems, such as the Pamlico–Albemarle Sounds complex, local response to wind forcing is ultimately dependent upon inlet location and orientation. In North Carolina, sustained-flooding or ebbing events are associated with the passage of atmospheric low pressure systems that occur at an average rate of four each month from November to April (Cione et al., 1993). Coincidentally, winter is the main immigration season for ocean-spawned fish species of commercial importance (Hettler & Chester, 1990; Warlen & Burke, 1990).

In 1993, Smith & Stoner numerically simulated the transport of plankton that respond either to light intensity or to tidal phase. Their results suggested that even weak changes in tidal flow would greatly alter the net transport of larvae responding only to light. The same changes would not significantly affect retention of the latter. An experiment attempting to determine the influence of flow conditions on the retention of ichthyoplankton was implemented in Beaufort Inlet. Due to its position the inlet is relatively insensitive to meteorological forcing of water, and the semi-diurnal tidal regime is relatively regular (Klavans, 1983).

MATERIALS AND METHODS

Study area and sampling protocol

The Pamlico and Albemarle Sounds form a large estuarine complex located on the eastern coast of the USA (Figure 1). The system connects to the Atlantic Ocean through four major inlets. The sampling site was located at the Pivers Island Bridge that crosses a small side-channel ~2 n.m. (3.8 km) inland of Beaufort Inlet (34°43′N 76°40′W) (Figure 1).

Sampling was performed with a conical net of 1000-μm mesh fitted with a removable cod-end. The size of the net
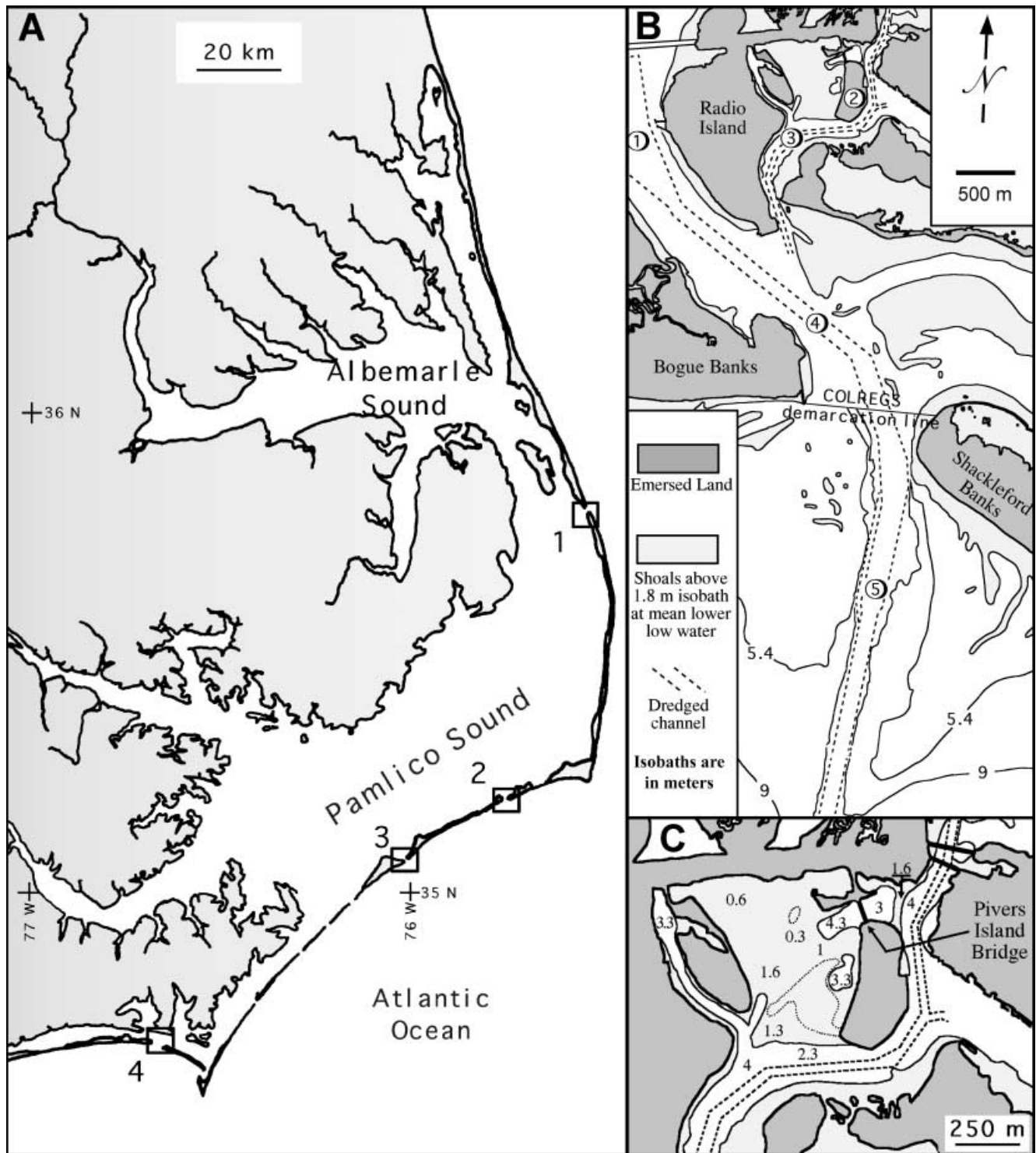
Figure 1. (A) Geographic location of Pamlico and Albemarle Sounds. The four major inlets into the estuarine system are numbered: 1, Oregon Inlet; 2, Hatteras Inlet; 3, Ocracoke Inlet; and 4, Beaufort Inlet. (B) Beaufort Inlet. Circled numbers indicate landmarks and submarine features: 1, turning basin of the State Port Terminal; 2, Pivers Island; 3, Beaufort Channel; 4, Morehead City Channel; and 5, Beaufort Inlet Channel. The 18 ft (5.4 m) and the 30 ft (9 m) isobaths are indicated. (C) Detail of the area surrounding the sampling site: arrow, Pivers Island Bridge; dotted lines, shoals emerged at low tide. Depth (m) at mean lower low water (MLLW).

opening was computed to retain only what it could hold in the cod-end. Previous tests (at Oregon Inlet) had demonstrated that a 60-cm diameter net can be overwhelmed by larvae during specific meteorological events. Thus, the original 60-cm diameter bongo frame was equipped with a collar that reduced the mouth opening to 27.5 cm in diameter. The skirt of the collar was made of the same mesh as the net. A high-speed flowmeter was attached to the sampling gear. Two seven-digit, intercalibrated flowmeters were used during the experiment. A 20 kg weight tied to the ring, opposite to the retrieving rope, ensured that the net mouth remained in vertical position. Except for the last metre of the net (including the cod-end), the net was maintained open and horizontal in the water.

Thus, the sampling depth was set constant at ~ 2 m above the bottom and ~ 1.8 and 2.4 m below the surface at low tide and high tide, respectively. Each tide was completely sampled to accommodate for the asynchrony among species caused by the overlay of a diel and, often, a tidal rhythm of vertical migration within the water column (Joyeux, 1998). Setting and retrieval of the net was performed at each actual slack tide (no current), i.e. not at the predicted time of the slack tide (lowest or highest water level). Joyeux (1999) demonstrated that long passive samples (<32 min) are as efficient as short passive samples (4 min) to estimate larvae abundance, and that gear-avoidance is unrelated to fishing time. The same study showed that escape is unrelated to current speed at the sampling site. After retrieval, the net was rinsed, the cod-end exchanged with a new one, and the apparatus immediately re-set. When flowmeter malfunction was apparent (for example, filamentous algae wrapped around the rotor axle), the flowmeter was exchanged. Collected samples were immediately preserved in 90% alcohol. Mid-water salinity and temperature were recorded for each slack tide with a multiparameter YSI85. The experiment started on 10 March 1996 at 1910 hours and ended on 28 March 1996 at 1045 hours, sampling sixty-eight tides (i.e. 34 tidal cycles).

Collected data and preliminary computations

Larvae and early juveniles were identified and enumerated in the laboratory. Four species were abundant enough to support analysis: a clupeid Atlantic menhaden *Brevoortia tyrannus* (Latrobe, 1802), two sciaenids Atlantic croaker *Micropogonias undulatus* (Linnaeus, 1766) and spot *Leiostomus xanthurus* (Linnaeus, 1766), and a sparid pinfish *Lagodon rhomboides* (Linnaeus, 1766). All were early juveniles. N, is the number of larvae caught during the tide sampled. L, the length of the water tongue having flowed through the net during each tide (i.e. the distance travelled by the water under the bridge), was estimated from flowmeter readings. Due to flowmeter malfunction, five tidal cycles (eight tides) had missing values for flood, ebb or both tides. L-values were most likely underestimated since the high-speed flowmeter is not very efficient at low current speed.

Estimated height of tides (H_E) for Morehead City ($34.7183°$N $76.6950°$W) was obtained from a tide predictor program (Flater, 1997). Results furnished by the program were found to be in good accordance with data previously published by the NOAA (National Oceanic and Atmospheric Administration). The difference in height between slack tides was calculated (HD_E; Δh in Figure 2A). The (vertical) retention of water (R_E) was computed for each tidal cycle as

$$R_E = \frac{\Delta h_F - \Delta h_E}{\Delta h_F} = \frac{d}{\Delta h_F} \qquad \text{if } \Delta hF \geqslant \Delta hE \qquad (1)$$

or

$$R_E = \frac{\Delta h_E - \Delta h_F}{\Delta h_E} = -\frac{d}{\Delta h_E} \qquad \text{if } \Delta hF \geqslant \Delta hE \qquad (2)$$

where Δh_F is the expected difference in height between the beginning and the end of the flood, Δh_E is the difference between the beginning and the end of the ebb, and d is the

absolute value of the difference between Δh_F and Δh_E (Figure 2A). Negative values for R_E indicate more water exiting towards the ocean than entering towards the sound. In contrast, positive values indicate more water entering than exiting.

Observed water levels (H_D) were obtained from the water gauge (station 8656483) located at the Duke University Marine Laboratory, about 300 m from the sampling site. Difference in water level between slack tides (HD_D; Δh in Figure 2A) and vertical retention (R_D) at the Duke gauge were computed as previously described in eqns 1 and 2.

Horizontal retention of water (R_B) and retention of larvae (R_S) was computed for each tidal cycle (flood tide plus the following ebb tide) as

$$\text{Retention}_{Bridge,Species} = \frac{\text{Entering} - \text{Exiting}}{\text{Entering}}$$

$$\text{if Entering} \geqslant \text{Exiting} \qquad (3)$$

or

$$\text{Retention}_{Bridge,Species} = -\frac{\text{Exiting} - \text{Entering}}{\text{Exiting}}$$

$$\text{if Entering} < \text{Exiting} \qquad (4)$$

with Entering being the distance travelled by the water (L) or the number of larvae caught during flood tide (N), and Exiting the value for L or N during ebb tide. R_B, R_S therefore may vary between $+1.00$ (all that entered with the flood flow was retained inland of the sampling site) and -1.00 (all that exited during the ebb tide had not entered during the previous flood tide). A number of missing values were created for larval retention (R_S) when zero fish were caught during both flood tide and the following ebb tide. These missing values cannot be converted into zero-values (that are obtained when Entering=Exiting $\neq 0$). The option of 'reversing' eqn 3 into eqn 4 was chosen to stabilize the error variance: the values are then symmetrically distributed above and below zero. Otherwise, R_S would have varied between 0 (zero) and $-\infty$ (minus infinity) when larvae where captured in greater number during the ebb than during the previous flood tide. Note that eqns 3 and 4 are similar to eqns 1 and 2, respectively, and thus allow comparisons among the variables R_E, R_D and R_B, R_S.

Data for wind speed and direction recorded by the meteorological station (CLKN-7) located at Cape Lookout, North Carolina, ($34.62°$N $76.52°$W; ~ 15 km east of the sampling site) were obtained from the National Data Buoy Center (National Weather Service, NOAA). Ten-min interval vectors were summed for each actual tide (as recorded by the Duke gauge). The across-shore component of the wind (labelled NS) was estimated as the magnitude of the projection of the vector-sum on the north–south axis (i.e. vector length×cos(vector direction)). Similarly, the sine function furnished the along-shore component of the wind (EW). Since cos(vector direction) $=1$ indicates wind from true north, and sin(vector direction) $=1$ indicates wind from true east (Figure 2B), the sign of each component variable indicates the two quadrants from which the wind was blowing.
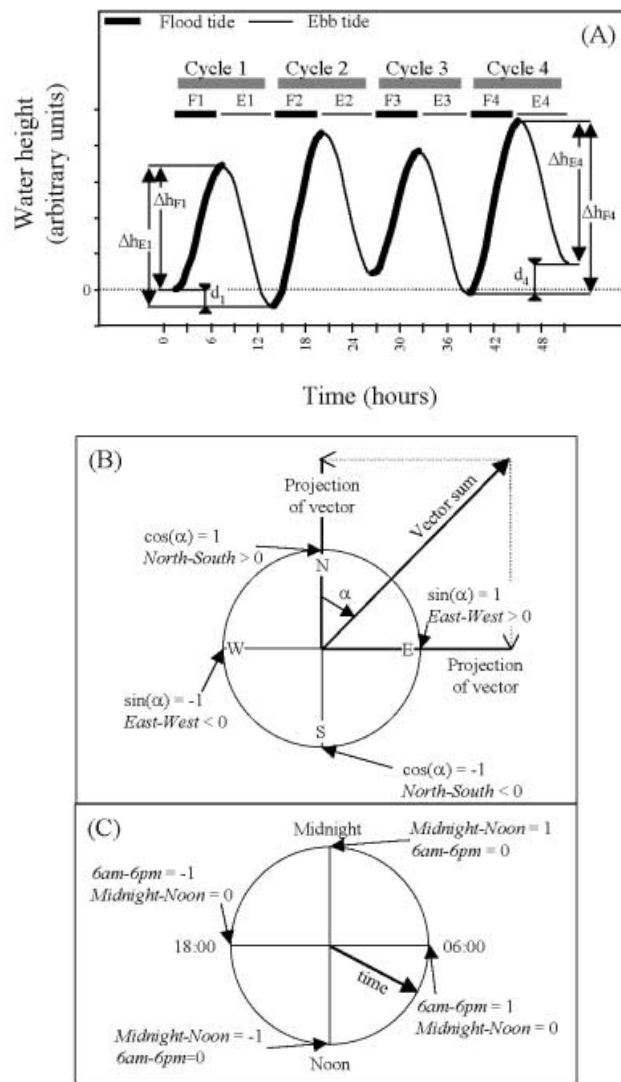
Figure 2. Diagrammatic representations for: (A) vertical retention of water. Tidal cycles 1 and 4 example the eqns 2 and 1, respectively. Δh, difference in height between the beginning and the end of the tide; d, absolute difference between Δh for the flood and Δh for the following ebb; (B) wind variables. The projections of the vector sum on the vertical and horizontal axes furnish the values for the variables north–south and east–west, respectively; (C) net-setting time was coded in the two variables M–N and 6–6.

Numerous fish larvae migrate vertically on a diel periodicity, yet this pattern often occurs in combination with a tidal migration. The non-pelagic croaker, spot (Weinstein, 1979; Weinstein et al., 1980; Lawler et al., 1988; Joyeux, 1998) and probably pinfish (Hettler & Barker, 1993; Forward et al., 1998) perpetuate rhythmic movements in respect to daylight and tide. These species are supposed to use TST to ingress from the ocean to the estuary. By contrast, the vertical migration pattern of pelagic menhaden mainly follows a diel periodicity without much regard to the tide direction (Joyeux, 1998). Thus the species is presumed not to use TST. The duration of the tide under night conditions and the distinction between beginning, ending, or complete tide are therefore important parameters to consider. No single variable can condense this information. Thus, it was summarized with two trigonometric variables coding for the time of net

setting (Figure 2C). M–N varies from +1 (midnight) to −1 (noon) while 6–6 varies from +1 (0600) to −1 (1800). Interpretation in relation to daylight conditions is facilitated by the fact that the sampling period was close to the spring equinox: sunrise occurred between 0625 and 0604 hours and sunset between 1812 and 1824 hours local winter time.

Statistical analysis

Autoregressive (autocorrelative) models were used extensively to determine to what extent a variable value recorded at a specific time (lag = 0) was dependent upon values at previous times (lag = 1, 2, ..., n). The time interval considered was one tide or one tidal cycle according to the dependent variable tested. Various models initially included independent (non-lag) variables. The general equation of the models was

$$D_{lag0} = Error + Intercept + a_1(Independent)$$
$$+ b_1(D_{lag1}) + \ldots + b_n(D_{lagn}) \qquad (5)$$

with D_{lag0}, D_{lag1} and D_{lagn} the tested variable value for, respectively, the time considered (lag = 0), the 1st lagged- and the nth lagged-time, and a_1, b_1, b_n the parameter estimates that minimize the error. Non-significant terms (α=0.05) were deleted from the model according to a backward removal process (SAS Institute, Inc., 1989).

Salinity and temperature at the end of each tide were tested in respect to wind (NS and EW). Four autoregressive terms (lags 1–4) for the dependent variable were initially included.

Models including the independent variable L were built to determine to what extent the number of fish (N) caught during a specific tide was dependent upon the tide flow and upon the number of fish entering or exiting during previous tides. Eight autoregressive terms (lags 1–8) were initially included.

Similar models were built for the retention of water (R_D, R_B) and larvae (R_S). The time interval considered was one tidal cycle. Only autoregressive parameters (lags 1–6) were included.

The relations between the observed retention (of water and larvae: R_B, R_D, R_S), the expected retention (R_E), the wind (north–south and east–west), and the setting time of the net (M–N and 6–6) were evaluated. The starting multilinear regression models included 5–8 independent variables since, for each tidal cycle, two tidal values for wind and setting-time variables were available. The models were reduced (Neter et al., 1990) according to a backward removal process where the least significant variable was deleted until all remaining variables were significant at α=0.05.

RESULTS AND DISCUSSION

Environmental conditions

According to water height, no difference in tide duration was apparent (Table 1). However, according to flow, the tide duration depended upon its direction: flood tides were 46 min shorter than ebb tides (Table 1). This may be due to ebb waters bypassing the sampling site (Figure 1).

Table 1. *Volume of water filtered by the net and duration of the tide.*

	N	Mean	Minimum	Maximum	SD	SE
Volume filtered (m³)						
All tides	60*	1177	256	2125	524	68
Flood	29*	1092	256	1938	514	95
Ebb	31*	1255	381	2125	528	95
Duration according to flow (Bridge)						
All tides	68	5 h 58 min	3 h 44 min	7 h 55 min	0 h 48 min	0 h 06 min
Flood	34	5 h 34 min	3 h 44 min	6 h 42 min	0 h 41 min	0 h 07 min
Ebb	34	6 h 22 min	5 h 18 min	7 h 55 min	0 h 41 min	0 h 07 min
Duration according to water height (Duke)						
All tides	68	6 h 14 min	5 h 12 min	7 h 42 min	0 h 29 min	0 h 06 min
Flood	34	6 h 17 min	5 h 18 min	7 h 42 min	0 h 29 min	0 h 09 min
Ebb	34	6 h 10 min	5 h 12 min	7 h 18 min	0 h 29 min	0 h 09 min

N, number; SD, standard deviation; SE, standard error; *, several tides had missing values for L due to flowmeter malfunction.
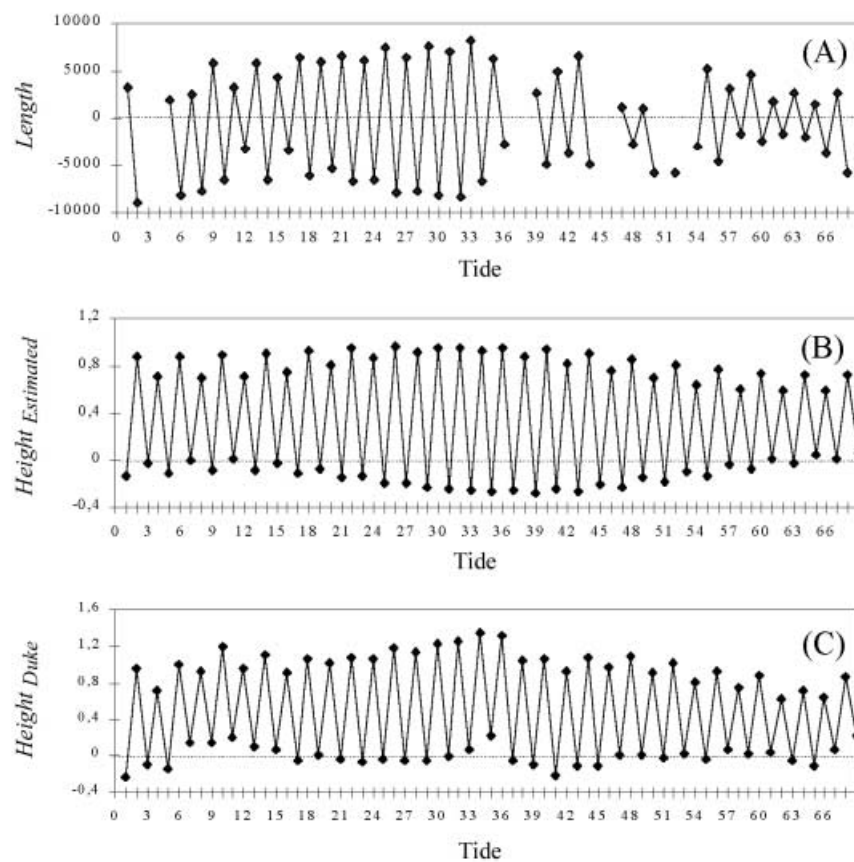
Figure 3. Recorded and estimated flow conditions. Tide 1 was a flood tide and tide 68 an ebb tide. (A) Length of the water tongue (L) filtered by the net sampling under Pivers Island bridge. Values were plotted positive for flood tides and negative for ebb tides; (B) expected height of the water in Morehead City Harbour at the beginning of each tide (H_E). The value for tide 69 corresponds to the end of tide 68; (C) water level recorded at the Duke gauge at the beginning of each tide (H_D).

Table 2. *Statistics for the linear models on observed water movements. All values are absolute, i.e. without indication of the flow direction (flood or ebb tide). All correlations were positive.*

Dependent Variable	HD_D			L		
	N	r^2	P	N	r^2	P
HD_E	68	0.90	0.001	60	0.30	0.001
HD_D	–	–	–	60	0.25	0.001

N, number; *r*, correlation coefficient; *P*, probability.

Table 3. *Statistics for the multilinear models on the observed water movements. Values for the variables are relative because wind differently affects flood and ebb flows. The plus or minus sign between parentheses indicates the sign of the correlation.*

Dependent	HD_D	L	L
N	68	60	60
P	$\leqslant 0.001$	$\leqslant 0.001$	$\leqslant 0.001$
Adj. r^2	0.99	0.90	0.90
Variables	(sign) pP	(sign) pP	(sign) pP
Intercept	ns	ns	ns
HD_E	(+) 0.001	(+) 0.001	Not included
HD_D	Not included	Not included	(+) 0.001
North–south	(+) 0.001	(−) 0.004	(+) 0.001
East–west	–	–	–

pP, partial probability; ns, non significant; −, non-significant and removed from the model.

Table 4. *Statistics for the autoregressive models on salinity and temperature recorded at the end of each tide. The dependent variable is $Parameter_{lag0}$. The plus or minus sign between parentheses indicates the sign of the correlation.*

	$Parameter_{lag0}$	
Dependent	Salinity	Temperature
N	63	65
P	$\leqslant 0.001$	$\leqslant 0.001$
Adj. r^2	0.90	0.84
Variables	(sign) pP	(sign) pP
Intercept	(+) 0.019	(+) 0.001
North–south	(−) 0.016	(−) 0.001
East–west	–	(+) 0.006
$Parameter_{lag1}$	(+) 0.001	–
$Parameter_{lag2}$	(+) 0.001	(+) 0.001
$Parameter_{lag3}$	(−) 0.001	–
$Parameter_{lag4}$	(+) 0.003	(+) 0.001

pP, partial probability; –, non-significant and removed from the model.
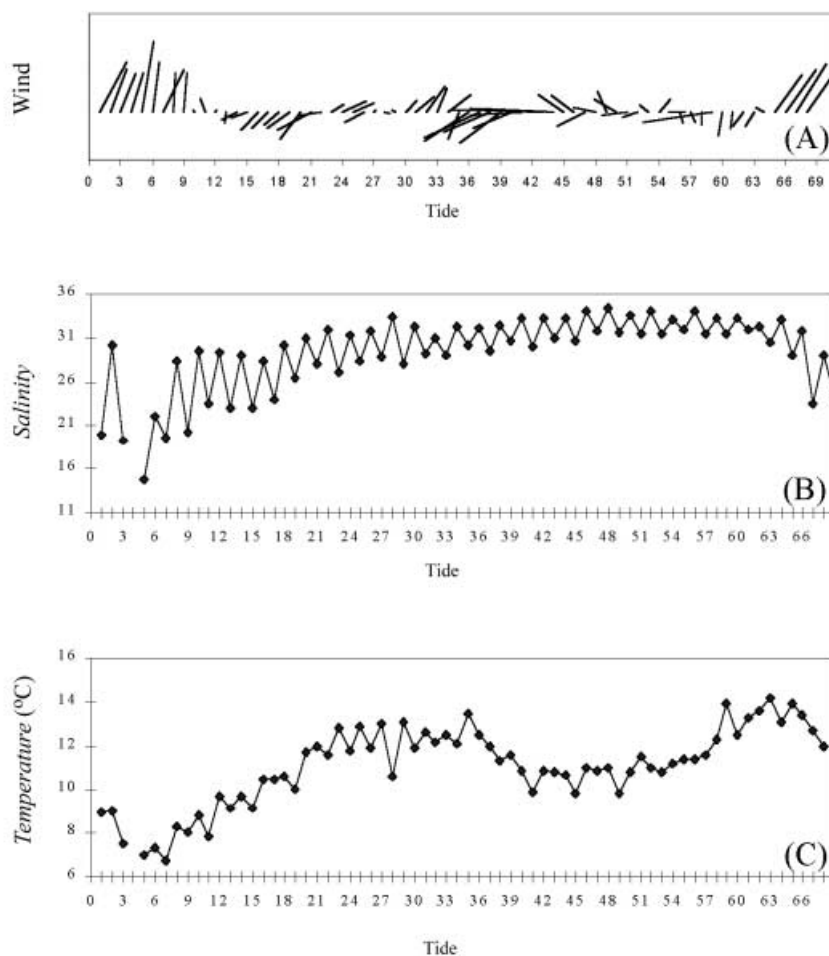

Figure 4. Recorded environmental conditions. Tide 1 was a flood tide and tide 68 an ebb tide. (A) Wind vector sums for each tide. Vectors are plotted in the direction from which the wind blew; (B) salinity at the beginning of each tide. Tide 69 corresponds to the end of tide 68; (C) water temperature at the beginning of each tide.

Table 5. *Statistics for the multilinear models on the number of migrating individuals of each taxa in function of net-setting time. The plus or minus sign between parentheses indicates the sign of the correlation.*

Dependent	*Brevoortia tyrannus*	*Leiostomus xanthurus*	*Micropogenias undulatus*	*Lagodon rhomboides*
N	68	68	68	68
P	0.001	0.001	0.001	0.001
Adj. r^2	0.15	0.24	0.36	0.16
Variables	(sign) pP	(sign) pP	(sign) pP	(sign) pP
Intercept	(+) 0.001	(+) 0.001	(+) 0.001	(+) 0.001
M–N	(+) 0.001	(+) 0.001	(+) 0.001	(+) 0.001
6–6	–	–	(−) 0.008	–

pP, partial probability; –, non-significant and removed from the model; M–N, midnight to noon; 6–6, 0600 to 1800.
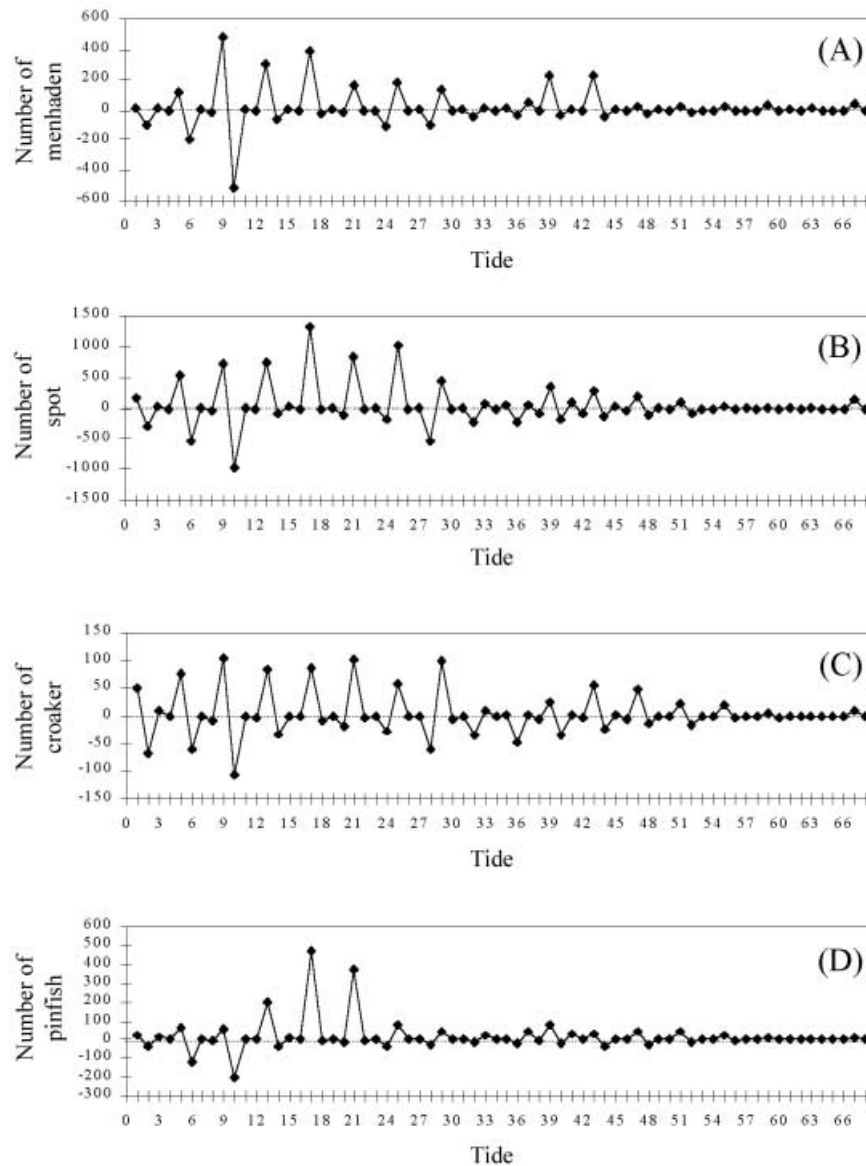
Figure 5. Number of larvae caught during each tide sampled (N). Values were plotted positive for flood tides and negative for ebb tides. (A) Menhaden *Brevoortia tyrannus*; (B) spot *Leiostomus xanthurus*; (C) croaker *Micropogenias undulatus*; (D) pinfish *Lagodon rhomboides*.

Table 6. *Statistics for the autoregressive models on the number of migrating individuals of each taxa (i.e. the dependent variable is* $Number_{lag0}$*). The plus or minus sign between parentheses indicate the sign of the correlation.*

| Dependent | $Number_{lag0}$ | | | |
	Brevoortia tyrannus	*Leiostomus xanthurus*	*Micropogonias undulatus*	*Lagodon rhomboides*
N	54	54	54	54
P	0.001	0.001	0.001	0.001
Adj. r^2	0.39	0.58	0.68	0.55
Variables	(sign) pP	(sign) pP	(sign) pP	(sign) pP
Intercept	(+) 0.049	ns	ns	ns
L*	–	–	–	–
$Number_{lag1}$	(+) 0.032	–	(+) 0.033	–
$Number_{lag2}$	–	–	–	–
$Number_{lag3}$	–	–	–	–
$Number_{lag4}$	(+) 0.001	(+) 0.001	(+) 0.001	(+) 0.001
$Number_{lag5}$	(−) 0.008	–	(−) 0.046	–
$Number_{lag6}$	–	–	–	–
$Number_{lag7}$	–	(+) 0.020	(+) 0.009	–
$Number_{lag8}$	–	–	–	(−) 0.005

pP, partial probability; ns, non significant; –, non-significant and removed from the model; *, significance levels are similar if using HD_D instead of L, with the exception of $Number_{lag7}$ becoming significant (+; P=0.047) for *L. rhomboides*.
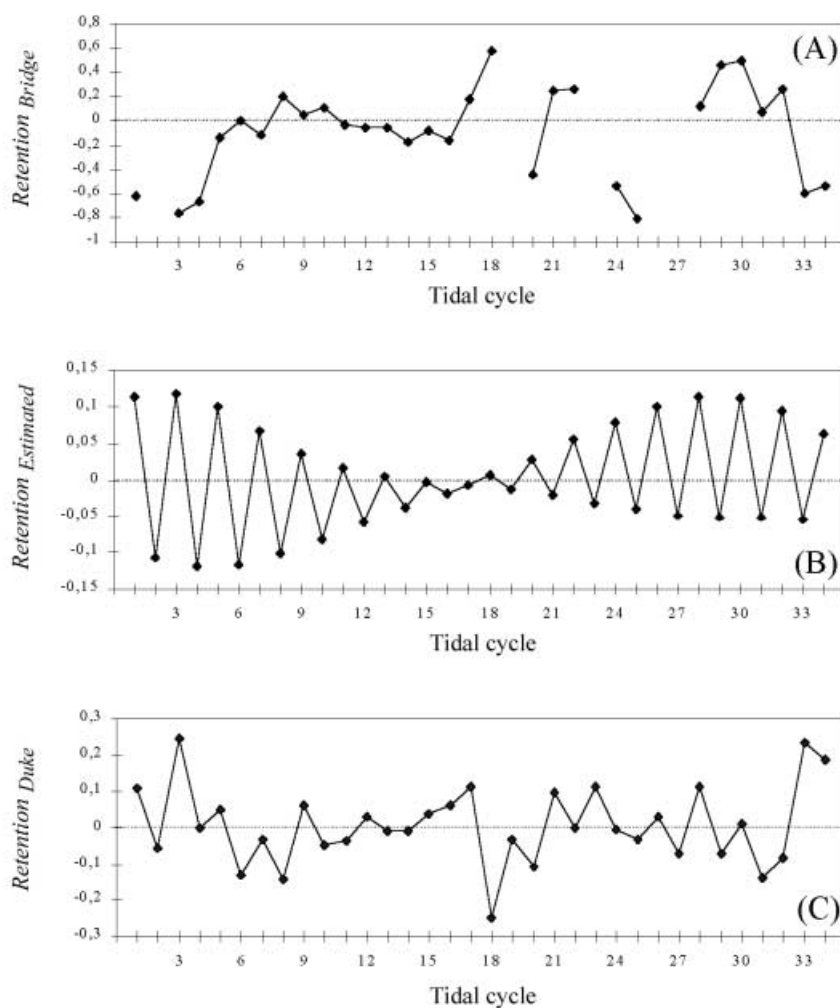
Figure 6. Recorded and estimated water retention. Positive numbers indicate more larvae entering than exiting. Negative numbers indicate more larvae exiting than had entered with the flood. (A) Horizontal water retention at the sampling site (R_B). Missing values were caused by flowmeter malfunction; (B) predicted vertical retention in Morehead City Harbour (R_E); (C) observed vertical retention at the Duke gauge (R_D).
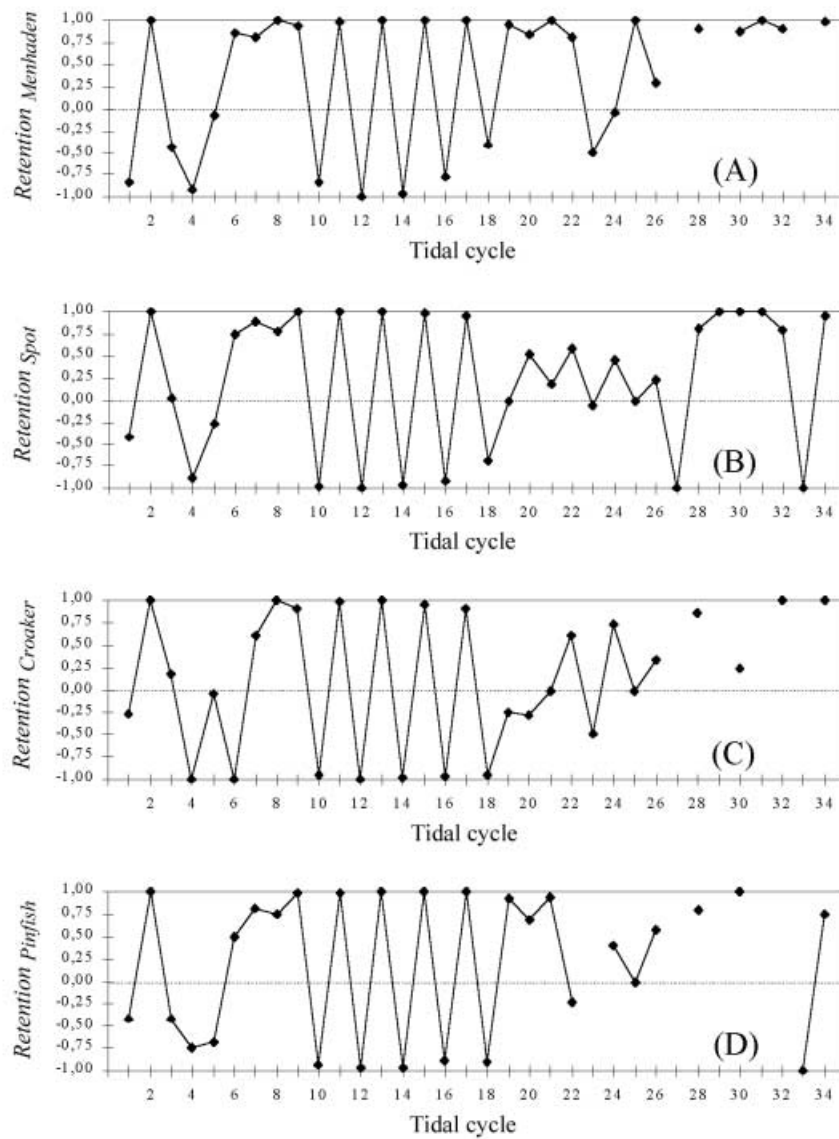
Figure 7. Larval retention (R_S). The absence of larvae during both tides caused missing values. Positive numbers indicate more larvae entering than exiting. Negative numbers indicate more larvae exiting than had entered with the flood. (A) Menhaden *Brevoortia tyrannus*; (B) spot *Leiostomus xanthurus*; (C) croaker *Micropogonias undulatus*; (D) pinfish *Lagodon rhomboides*.

Table 7. *Statistics for the autoregressive models on the retention of water and larvae (i.e., the dependent variable is Retention$_{lag0}$). The sign of correlation is given between parentheses.*

	Retention$_{lag0}$					
Dependent	Bridge (flow) R_B	Duke (height) R_D	*Brevoortia tyrannus*	*Leiostomus xanthurus*	*Micropogonias undulatus*	*Lagodon rhomboides*
N	21	30	25	30	24	23
P	0.001	0.008	0.032	0.020	0.007	0.001
Adj. r^2	0.72	0.20	0.19	0.18	0.30	0.45
Variables *	(sign) pP	(sign) pP	(sign) pP	(sign) pP	(sign) pP	(sign) pP
Intercept	ns	ns	ns	(+) 0,018	ns	(+) 0.012
Retention$_{lag1}$	(+) 0.001	–	–	–	–	–
Retention$_{lag2}$	(−) 0.001	–	(+) 0.032	–	–	–
Retention$_{lag3}$	(+) 0.001	(−) 0.008	–	(−) 0.020	(−) 0.007	(−) 0.001
Retention$_{lag4}$	(−) 0.001	–	–	–	–	–

pP, partial probability; –, non-significant and removed from the model; *, Retention$_{lag5}$ and Retention$_{lag6}$ were not significant in any of the models.

Table 8. *Statistics for the multilinear models (Type II) on the retention of water and of the four species. The sign of correlation is given between parentheses.*

Dependent	Retention					
	Bridge (flow) R_B	Duke (height) R_D	*Brevoortia tyrannus*	*Leiostomus xanthurus*	*Micropogonias undulatus*	*Lagodon rhomboides*
N	29	34	31	34	30	29
P	0.001	0.001	0.003	0.002	0.001	0.001
Adj. r^2	0.51	0.54	0.29	0.24	0.37	0.45
Variables	(sign) pP	(sign) pP	(sign) pP	(sign) pP	(sign) pP	(sign) pP
Intercept	ns	ns	(+) 0.001	(+) 0.041	ns	(+) 0.009
R_E	−	(+) 0.003	Not included	Not included	Not included	Not included
NS_E	(−) 0.001	(+) 0.001	−	−	−	−
NS_F	−	−	(−) 0.037	−	−	(−) 0.018
$M–N_F$	Not included	Not included	(+) 0.003	(+) 0.002	(+) 0.001	(+) ⩽0.001

Both water retention models included: NS_E, north–south ebb; NS_F, north–south flood; east–west ebb, east–west flood, and R_E, retention estimated. Larval retention models included the four wind variables previously listed and the four variables indicating the time of net setting: $M–N_F$, $M–N_E$, $6–6_F$, $6–6_E$. pP, partial probability; −, non-significant and removed from the model.

The length of the water tongue filtered by the net varied widely (Figure 3A). The fortnightly and semi-diurnal rhythms, characteristic of astronomical tides in the region, were apparent, although altered (Figure 3A–C). Estimated and observed variation of the water level were strongly correlated (Table 2). The north–south component of the wind strongly affected the vertical and horizontal movements of the water, although in opposite directions (Table 3). The apparent contradiction is easily explained. Under northerly winds, Sound waters pile up on the inner side of the inlet and fall down on the ocean side. This induces high-tide water level to increase, flood current to weaken, low-tide level to decrease, and ebb current to strengthen. The reverse would be true under southerly winds. Thus, vertical amplitude appears to be a poor indicator of horizontal movement. Actually, 25% of the variability in L (partial correlation with NS = 0.50, controlling for HD_D) was explained by across-shore winds. Since horizontal movements are ultimately responsible for horizontal transport, most of the following analyses are based on the variable L.

The effect of wind upon the physico-chemical characteristics of the water was apparent (Table 4). North winds induced a lowering of salinity and temperature (Figure 4A–C). Less salty and cooler estuarine waters replaced the usual little-diluted oceanic waters. West winds lowered the temperature but did not induce salinity change (Table 4). Tentatively, this feature is attributed to along-shore water movements within Core Sound.

Larval collection

The four species presented a clear diel rhythm of capture: fewer larvae were caught during daylight (Table 5). Higher numbers were caught when the net was set near midnight (all species) or near sunset (croaker). The number of larvae entering or exiting diminished towards the end of the experiment (Figure 5A–D). Tides 1–14 occurred under conditions similar to those of tides 55–68, with respect to flow, wind direction, daylight, lowered salinity and temperature. In spite of this, the number of larvae caught was much lower during the latter period

than during the former, indicating that the diminution should be regarded as resulting from a decrease of larval availability, and not as an avoidance or escapement bias.

For all species, the number of larvae caught during a specific tide was strongly correlated with the number of larvae at lag = 4 (Table 6). This was not surprising considering that 0- and 4-lagged tides occur in similar conditions of current (flood or ebb) and circadian period (night or day). Additionally, weaker correlations were evidenced with lags = 1, 5, 7 and 8.

Water and larvae retention

The horizontal retention of water (Figure 6A) had little relation with the larval retention that could shift from +1 to −1 from one tidal cycle to the next (Figure 7A–D). Similarities among species were obvious for the tidal cycles 10–18. These cycles were coincidental with an important decrease in variability of the expected retention (Figure 6B), and to alternate shifts from night flood+day ebb (with retention ∼ +1) to day flood + night ebb (retention ∼ −1). Horizontal retention of water was autocorrelated up to lag=4, while vertical retention was only autocorrelated at lag=3 (Table 7). Significant autocorrelations for larval retention were limited to either the second or third lag, i.e. the cycles that had occurred during the previous 24 h (similar conditions: menhaden) or 36 h (opposite conditions: spot, croaker and pinfish). The observed vertical retention of water (R_D), and retention of non-pelagic species were autocorrelated with the same lag (lag=3; Table 7).

The vertical retention of water was predicted to follow a fortnightly and semi-diurnal periodicity (Figure 6B), with the highest variability between following tidal cycles occurring at the beginning and at the end of the experiment. However, the horizontal retention of the water at the sampling site was solely dependent upon the across-shore component of the wind that affected the ebb tide (NS_E; Table 8). Thus, horizontal retention was essentially determined during ebb tides, favoured by northward wind while unfavourably affected by southward wind. Those winds also affected the water level in the expected

manner (Figure 6C and Table 8). Along-shore winds, from east or west, showed no significant effect on water or larval retention.

Initial regression models for the larvae of the four species included all wind variables. To account for non-meteorological variability, the variables coding for the time of net-setting were also entered. The retention of all species was correlated with flood sample beginning in the middle of the night (Table 8), i.e. retention was highest in cycles presenting a night flood sample followed by a day ebb sample. Retention of menhaden and pinfish increased with northward winds and decreased with southward winds that occurred during flood tides (Table 8).

An estimate of the duration of carry-over (up- and down-estuary movement of larvae 'trapped' in flood and ebb flows within the inlet's boundaries) can be obtained from the number of the last autocorrelated tide (Table 6) or autocorrelated tidal cycle (Table 7). Carry-over did not extend for more than two days. The shortest carry-over time was recorded for menhaden (five tides, i.e. ~1 d) and the longest for spot, croaker and pinfish (seven and eight tides, i.e. ~2 d).

For the whole sampling period, the larval retention past the sampling site varied from $+0.32$ for croaker to $+0.60$ for pinfish. Menhaden ($+0.47$) and spot ($+0.48$) were intermediate.

Tidal stream transport-using species migrate down towards the slow-ebbing bottom currents to avoid being flushed too far back by ebbing flows. They move up from the bottom when the conditions of light intensity and flow direction are again favourable. Spot and croaker perpetuate these vertical movements (Weinstein et al., 1980; Lawler et al., 1988; Joyeux, 1998) and, supposedly, use TST. Tentatively, findings on these species can be extended to other TST-using species. 'New' immigrants are considered to be the larvae entering the inlet for the first time and 'old' immigrants those that have already undergone one or several tidal cycles but are still within reach of flood flow. The 'new' larvae that interrupt their landward migration when light or flow conditions become adverse or unfavourable can resume their landward motion ~18 h later in areas of semi-diurnal periodicity (i.e. at the beginning of lag = 4). If still unsuccessful, they can try again ~42 h after their first attempt (i.e. at lag = 8). These now 'old' larvae may or may not mix with 'new' ones but any given situation will repeat itself with little change from one night to the next (Table 6). Thus, there can be a simultaneous presence of several (three at the most in our case) waves of immigrants in the catches. According to the results in Table 6, there is no fourth attempt, and larvae are then either definitively retained or definitively lost. Presumably, meteorological conditions do not greatly affect the transport, carry-over, or retention of TST-using species since larvae tend to remain in least-affected (deepest) water masses during the ebb tides. Accordingly, the retention of sciaenid larvae inland of the sampling site was independent from advantageous or disadvantageous wind forcing conditions alike (Table 8).

In contrast to spot and croaker, menhaden does not migrate vertically in response to tide reversal (Joyeux, 1998). Between dusk and dawn larvae distribute within the inlet's whole water column without regard to the flow direction. Species that appear not to use TST tend to be

flushed into the ocean by ebbing currents when the ebb tide occurs during night time (Smith & Stoner, 1993) or when flood flow is weaker than ebb flow. Since a small offset in the balance of strength between flood and ebb can be beneficial (or detrimental) to these species, any favourable (or unfavourable) meteorological condition will improve (or reduce) entry and retention. Indeed, menhaden retention was significantly correlated to wind on the longitudinal axis (north–south) of the inlet (Table 8). This also translates to significant autocorrelations at lower lags (Tables 6 & 7). Thus, larvae that migrate upward without regard to the flow direction appear to be extremely sensitive to wind-induced perturbations.

Pinfish retention was clearly dependent on wind strength and direction (Table 8), while otherwise the species seemed to behave like the sciaenids, i.e. like a TST-using species (Table 7). Field results (Hettler & Barker, 1993; Forward et al., 1998) were not clearly conclusive. Laboratory experiments (Forward et al., 1998) evoked for this species and others (references cited in the study), increased swimming activity for both ascent during night-time (circadian rhythm) and descent during ebb tides (tidal rhythm), which is not contradictory but somewhat surprising.

Unless astronomical tides are totally overwhelmed, it is generally assumed that the vertical positioning of immigrating larvae is one of the most important factors for entry and retention. During the experiment, maximum sustained winds were about 10 ms^{-1} (36 km h^{-1}). Within this three-week time frame, the retention of TST-using species was independent of relatively clement weather conditions and that of non-TST was dependent. However, no evidence has been found that tidal-rhythmic vertical migrations (i.e. TST) 'improves' retention, or that non-tidal vertical migrations (i.e. non-TST) in comparison worsens retention. One of the TST-using, non-pelagic species (Atlantic croaker) unexpectedly showed the lowest retention. Admittedly, the bathymetry at the sampling site could have forced bottom-ebbing larvae to bypass the sampling site (Figure 1), a feature that probably greatly improved the retention calculated for TST-using larvae. The ambiguous species (pinfish) showed the highest retention. Differences observed between these two species cannot be easily related to swimming ability since both are of similar size (Hettler, 1997; Hettler & Hare, 1998). The two remaining species, one TST-using, non-pelagic (spot), and the other non-TST, pelagic (menhaden) showed intermediate retention, similar to each other.

It appears that selective tidal stream transport does not seem to be necessary for larvae to ensure entry and retention within the estuary. In fact, the fortnightly periodicity in abundance previously observed for all species except pinfish, and the coincidental influence of tidal amplitude and current for menhaden and pinfish (Hettler et al., 1997), already indicated the fundamental importance of flow.

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